THE GENESIS OF FAULT-BARS IN FEATHERS AND THE CAUSE OF ALTERNATION OF LIGHT AND DARK FUNDAMENTAL BARS.

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With 4 Plates and 5 Figures in the Text.

CONTENTS.

INTRODUCTION.

During recent years several attempts have been made to find a basis, structural or physiological; for the color patterns of various animals. Among the most notable and successful of these

may be cited the studies of Graf[1] on leeches and of Loeb[2] on fish embryos. Graf was able to show that the characteristic markings of the leeches examined depend primarily upon the number and arrangement of the muscles of the body-wall. Loeb showed that in *Fundulus* embryos, markings are produced by a grouping of pigment-cells around the blood-vessels. The present paper is chiefly a report of observations and experiments which furnish a physiological basis for what seems to be the primitive color-markings of the feathers of birds.

This research was undertaken at the suggestion of Professor C. O. Whitman; it is here a pleasure to thank him for much kindness and encouragement and to acknowledge the great value of his help and criticism.

Two observations by Professor Whitman furnished the starting point for these studies; first, there is in all feathers a "fundamental barring" of the whole length of the feather; second, certain defects (fault-bars) occasionally appear in the plumages of birds reared under adverse conditions. In presenting the facts which furnish a physiological basis for these two characters, it seems best to consider the fault-bars first, since they furnish the key to an understanding of the fundamental bar.

The Morphology of Fault-Bars.

I have found five types of defects and have made it certain that they all really represent the same thing. Two of these types were seen and described by Strong[3] from a hybrid pigeon. Duerden[4] has also reported one of the types described by Strong as occurring in great numbers in ostriches. These defects have doubtless been seen by several naturalists. Darwin came across them in at least two instances. He cites[5] some variations in the

[1] Graf, Arnold, "Ueber den Ursprung des Pigments und der Zeichung bei den Hirudineen," *Zoöl. Anz.*, XVIII., 1895.

[2] Loeb, Jacques, "A Contribution to the Physiology of Animal Coloration," *Journal of Morph.*, Vol. VIII., 1893.

[3] Strong, R. M., "A Case of Abnormal Plumage," Biol. Bull., Vol. III, November, 1902.

[4] Duerden, J. E., "Bars in Ostrich Feathers," *Agr. Jour.*, Cape of Good Hope, May, 1906.

[5] Darwin, Charles, "The Variation of Animals and Plants under Domestication," Vol. I., p. 267.

hackles of a sub-variety of the game-cock in which "the tips having a metallic lustre are separated from the lower part of the feather by a symmetrically shaped, 'transparent zone' composed of the naked portions of the barbs." In another work[1] he describes the "transparent zone" of the ocellus of the peacock's

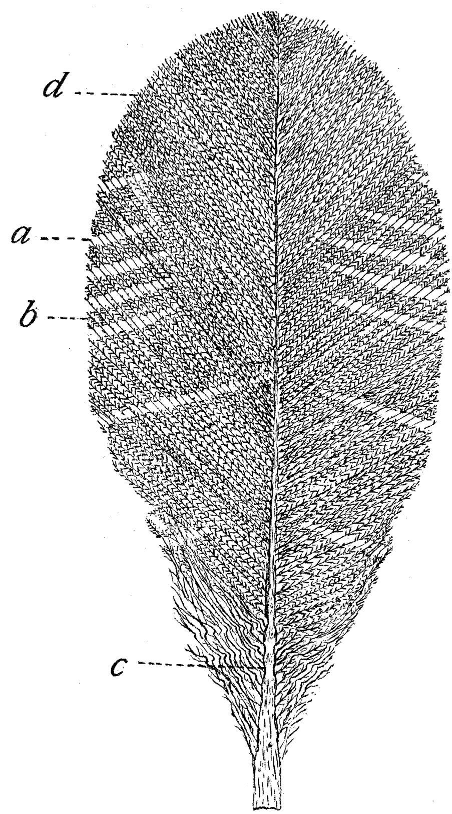

FIG. 1. Feather from a poorly nourished chick showing abnormalities. *a*, abnormal area; *b*, "fundamental bar" (a day's growth); *c*, constrictions; *d*, region in which defective lines showed plainly in this feather. × 2.

feather. Both of these belong to the sort of structure now under consideration.

Since so little has been said of these defects, and since their significance has nowhere been recognized, it seems advisable to give a very complete and detailed description of them. Such a

[1] Darwin, Charles, "The Descent of Man," 1871.

detailed account is, moreover, made imperative because of the basis which it supplies for a later consideration of the origin of color characters. A short description has already been published by the writer[1] in a preliminary statement of the results which are here given in full.

The Adult Feather. — The first type of these defects is to be found in the large and rapidly grown feathers of birds. The defect consists in the total or partial absence of barbs from definite transverse areas extending across the feather-vane, these areas making with the shaft or rachis an angle always the same — approximately, but not exactly, a right angle. A cross-section of the feather at this point would show only shaft and barbs. One such area in the entire length of the feather was one of the types described by Strong. I find, however, an abundance of cases where such areas occur at regular intervals, practically throughout the length of the feather. This regularity of the spaces separating the defects furnished, indeed, the clue to the nature of the latter. Fig. 1 shows a feather from a poorly nourished chick, in which a number of pronounced defects of this type occur. As stated above and as shown in the figure, defects of this type occur more frequently in rapidly grown feathers, and principally in the distal parts of these. Many of these defects may be seen in Pls. XIII. and XIV.

The second type represents the greatest extreme to be met with among these abnormalities. The feather in the abnormal region has been reduced to shaft only; both barbules and barbs are gone. The second of the defects described by Strong evidently belongs to this type, though he states that there was no shaft present in his material and that its place was taken by a small cylinder of fused barbs. I have not seen just such a structure as he describes.

Fig. 2, however, represents something which is, I think, entirely comparable. At *a* is seen a region in which shaft only is present. This part of the shaft is without pigment, although the distal and proximal parts of the shaft are heavily pigmented. We may regard such defects as a sort of record of the very sev-

[1] Riddle, Oscar, "A Study of Fundamental Bars in Feathers," BIOL. BULL., Vol. XII., February, 1907.

erest conditions which a bird can encounter and endure. In types 1 and 2, the barbs and shaft are often bent or kinked in the abnormal region.

The third type of defect is something very much less conspicuous than either of the two types just considered. It cannot be represented in a drawing. It is a very minute depression or differentiation of some sort extending across the surface of the feather in exactly the same direction as do the defective areas of type 1. It is not always easy, however, to determine that it is a depression at all. It often seems to be a line, or simply a point of union of the distal with the proximal part of the feather-vane. This line is sometimes so inconspicuous that even close observation may not reveal it. It is probable that these lines are not always depressions; but, that differences in light-reflecting power exist between a point in such a line and points anterior and posterior to it, is unquestionable.

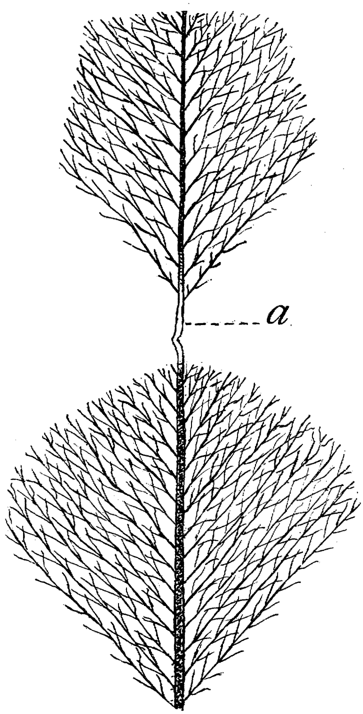

FIG. 2. Abnormal region of a plume from an ostrich chick (kindly sent to me by Prof. Duerden). *a*, fault-bar, type 2, in which shaft only is present. This region shows also a great reduction of the pigmentation of the shaft. $\times$ 4.

The term "line," is moreover, not a thoroughly satisfactory one, for, that these defects intergrade with others of appreciable *width* is certain. These lines are thoroughly characteristic of the feather and are properly classified among feather defects, for it is at such joints that defects like those of types 1 and 4 appear.

Many feather-vanes show at certain points in their length very deep depressions or constrictions which give to them a wavy appearance. At first sight such modifications have nothing in common with types 1 and 3, but closer study proves that they

stand for the same thing, and they are here classed as type 4. A wild *Cardinalis virginianus* brought from Florida threw, at the time of its first moult in captivity, feather-germs (Fig. 3) which were deeply constricted; when these expanded they presented the extremely wavy appearance shown in Pl. XIII., Fig. 9. The complete history of these defects from the time of their appearance about August 30 until October 15, 1906, was obtained. This material was secured through the kindness of Dr. Strong. The production of the extreme constrictions in the feathers of this bird is doubtless to be associated with its captivity and confinement in a cage. A longitudinal section of one of these feather-germs is to be seen in Pl. XII., Fig. 3, and the photograph of an entire feather in Pl. XIII., Fig. 9. The longitudinal section shows at "*a*" an indentation of the pulp cavity by the epidermal layers.

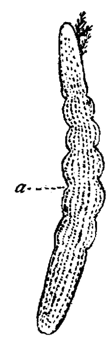

FIG. 3. × 3.

It will be noted that in all of these defects there is a weakening of the feather at successive levels in its length; or to state it more adequately, in all of these four types certain parts of the feather-vane are absent, weakened, or modified. The three parts of the feather — *i. e.*, barbules, barbs, and shaft — are, however, unequally and rather differently affected. The *barbules* may be absent (type 1), or merely weakened (type 3); the *barbs* may be absent (type 2), weakened, or kinked (type 4); the *shaft* or *rhachis* may be constricted and weakened (type 4). See text Fig. 1 and Pl. XII., Fig. 3. It will be observed too that all of the above defects — to which we apply the general term *fault-bars* — are extended upon the transverse axis of the feather. In one case I have found a weakening on one side of the feather-vane extending across many barbs in such a way as to produce a longitudinal fault-bar. Duerden[1] reports this as a rare occurrence in ostrich plumes. This furnishes us type 5 and is photographed in Pl. XIV., Fig. 23.

From what has been said, the relation between the first four types of defects is apparent. The importance attaching to the equivalence of types 1 and 3, however, merits particular notice. That they *are* equivalents is certain. The evidence in part is,

[1] *Loc. cit.*

that one sees all possible intergradations, that each marks off a day's growth, that when the area of type 1 occurs it always falls in the place for the line, that a certain part of the line only may be transformed into the obviously defective area, etc. Type 5 is probably caused by a protracted defective nutrition of a segment of the circle of growing feather-elements in the germ.

In connection with these fault-bars we may mention another condition met with in some extreme cases in which abnormalities extend almost continuously over several millimeters of the feather's length. There occurs not only a weakening of the parts, but also a lack of differentiation of the feather-elements. This is well shown by feathers from the nape of a chick which had been fed with Sudan III. In this case the inner and outer sheaths failed to separate from the barbs, and a banded condition results. Another example of such a structure grown in nature by an English sparrow is shown in Pl. XIII., Fig. 11. The lack of differentiation, curiously enough, occurs in only two rectrices and these were corresponding ones on opposite sides of the tail. Pl. XIII., Fig. 12, shows also an adjoining rectrix. The latter betrays by its similarly placed fault-bars the fact that they were both produced by the same cause. I have found similar bands on feathers from the head of the cardinal. They were being produced simultaneously with deep constrictions in the other feathers of the bird.

The Feather-germ. — The more prominent defects have been observed in the feather-germ, both in their initial stages and immediately before the breaking away of the containing sheaths and the unfolding of the feather-elements. The less conspicuous defective lines (type 3) have, however, escaped all observation in the germ, as indeed they have done in the adult feathers when the microscope was the means of observation. This apparently means that the modifications of such regions are extremely slight, not localized with extreme sharpness, and consist chiefly in slightly different powers to absorb or reflect light; this difference in reflecting power being better seen when the field of vision is large and the contrast between the parts of a large area plays a part.

The appearance of extreme constrictions on an expanded feather-germ has already been cited. The further fact that at

the constrictions in unexpanded germs the epidermal layers invade the parts normally occupied by the dermal pulp has also been referred to (Pl. XII., Fig. 3). Only another word concerning the histology of the defects need be said at this point, and the subject will be more fully discussed along with the cause of the defects. The normal development and histology is too considerable a subject to be considered here and the reader is referred to the papers of Studer,[1] Waldeyer,[2] Davies,[3] Haecker,[4] Maurer,[5] Strong[6] and others[7] for this information.

Much of feather structure is indicated in the plates of the present paper, but the description will deal only with such structures as are directly concerned with our own problem. The general relations of the parts of a feather in cross-section are shown in Pl. XII., Figs. 2 and 5.

The fault-bars in their earliest stages are indicated by a loose union of scattered cells in that part of the *intermediate* cell-layer which is forming the barbule cells. The cylinder-cell layer and apparently the more central cells of the intermediate cell layer (*i. e.*, those last formed from the cylinder layer) are crowded together as usual. Pl. XV., Fig. 26, represents some cellular relations at the close of a fault-bar producing period.

The Extent and Distribution of the Fault-Bars.

It has been stated that Professor Whitman was the first to direct attention to these abnormalities. He had observed them in some of his pigeons; one of these birds, a hybrid, furnished the material for Strong's[8] description of two types of defects

[1] Studer, T., "Die Entwicklung der Feder," Inaug.-Dissert., Berne, 1873. "Beiträge zur Entwicklungsgeschichte der Feder," *Zeit. f. wiss. Zoöl.*, Bd. 30, 1878.

[2] Waldeyer, W., "Untersuchungen ueber die Histogenese der Horngebilde, insbesondere der Haare und Federn," *Beiträge z. Anat. u. Embry. als Festgabe T. Henle*, Bonn, 1882.

[3] Davies, H. R., "Die Entwicklung der Feder und ihre Beziehungen zu andern Integumentgebilden," *Morph. Jahrb.*, Bd. 15, 1889.

[4] Haecker, V., "Ueber die Farben der Vogelfedern," *Arch. f. Micr. Anat.*, Bd. 35, Heft 1, 1890.

[5] Maurer, F., "Die Epidermis und ihre Abkömmlige," Leipzig, 1895.

[6] Strong, R. M., "The Development of Color in the Definitive Feather," *Bull. Mus. Comp. Zoöl. at Harvard*, Vol. XI., 1902.

[7] A very satisfactory bibliography to 1902 is given by Strong.

[8] *Loc. cit.*

already referred to. While this part of the present work was well on the way toward completion Professor Duerden[1] reported the "bars" (these are the exact equivalent of fault-bars of type 1) in the ostriches, and is at present attempting to rid those birds of them. He estimates that the value of the ostrich plumes from South Africa alone, are, by the presence of these defects, depreciated in value to the extent of £250,000 annually.

In the Bird Group. — The defects, however, are not confined to hybrid pigeons and domesticated ostriches. By simply looking for them it has been easy to find them everywhere. The *pronounced defects* of type 1 have been seen in parrots, trojans, owls, motmots, kingfishers, cuckoos, humming-birds, penguins, hornbills, turkeys, doves, chicks, English sparrows, herons, gulls, bluebirds, cardinals, robins, flamingoes, pheasants, loons, pea-cocks, etc.; everywhere, indeed, that I have looked for them except in fossil feathers, artists' drawings, and journals of ornithology! It will be seen that the defects occur in widely separated bird groups; in primitive and in recent birds; in land and water birds; in domesticated and in wild birds; in birds from the arctic and from the torrid zone, etc. I have been able, owing to the courtesies extended by Professor C. B. Cory and Dr. Ned Dearborn, of the Field Museum of Natural History in Chicago, to examine a very great variety of birds belonging to the Museum. I find that although it is not easy to see evident defects (*i. e.*, broad defective areas) in every specimen, it is easy to find them in every species. We may conclude, therefore, that they are to be found in *all* birds.

It is a fact, and a significant one I think, that the defects are, in general, more common in domesticated and caged birds than in wild birds. In this connection, however, it should be stated that the defects appear indifferently in pure breeds, hybrids and mongrels. At any rate I have verified this in a number of our domesticated birds. The effects of "inbreeding" have not been observed.

In the Various Plumages and Pterylæ. — I have found the emphasized defects in all of the plumages of birds, with the exception of the first or downy plumage. In some birds the

[1] *Loc. cit.*

defects seem to occur more frequently in the juvenal plumage (of Dwight) than in the others.

Evident defects appear in all the feather-tracts or pterylæ; but in a particular bird, and usually in a particular species, certain tracts show them in greater numbers than do others. In the ring dove, *Turtur risorius*, the order of frequency of occurrence is: rectrices, remiges, wing coverts, etc. In *Gallus* the order is: remiges, rectrices, wing or body coverts, etc.

In an Individual Feather. — In the feather there may be produced at any point in its length, either of the five types of abnormality. In some birds (*Gallus*) the distal part of the feather oftener shows the defective areas; the proximal end, the deep *constrictions* (type 4), while we get defective *lines* (type 3) in one form or another at all points in the feather's length.

The recognition of weakened areas as universal in feathers throws a new light on the rather over-discussed subject of feather *abrasion*. That there are birds whose feathers "normally" have the barbules broken off at certain fairly definite points in the more distal barbs has been observed by Meves,[1] Chapman,[2] Dwight[3] and others. Meves and Chapman have noted, too, that the barb itself may be broken near the distal end. I have seen several cases among wild birds of the breaking of a series of barbs at the point where they were crossed by the same defective line, and am convinced that further study will prove that most feather abrasions occur by the breaking away, as a single piece, of that portion of a barb which occupies the space between two fault-bars. That such breaks do occur at the fault-bars I have often proved by pulling the distal end of a series of barbs and noting the point at which they break. A feather treated in this way is shown in Pl. XIII., Fig. 7.

[1] Meves, W., "Über die Farbenveränderung der Vogel," *Jour. für Ornith.*, Bd. 3, 1855.

[2] Chapman, F. M., "On the Changes of Plumage in the Snowflake," *Amer. Mus. Nat. Hist.*, Vol. 8.

[3] Dwight, J., Jr., "The Sequence of Plumages and Moults in the Passerine Birds of New York," *Ann. N. Y. Acad. Sci.*, Vol. 13, No. 1.

THE EXPERIMENTAL PRODUCTION OF FAULT-BARS.[1]

Professor Whitman's suggestion that fault-bars are due to the malnutrition of the feathers during their growth, was put to a direct and vigorous experimental test. The method employed varied with the nature of the experiment and with the material, which was of four kinds. Of course, one had to work with *growing* feathers. Those experimented upon were (1) the juvenal feathers of ring doves (*T. risorius*); (2) the later plumages of ring doves produced at the regular season of moult; (3) feathers, chiefly remiges and rectrices, of ring doves obtained at any season by previously removing some of these; (4) juvenal and adult plumages of chicks (*Gallus*). All of these yielded entirely comparable results; the young birds merely showing a greater sensitiveness to lack of food. Five types of experiment were tried: (1) Reduced feeding or starving; (2) feeding with Sudan III.; (3) mechanical crumpling of the germs; (4) effect of light, temperature, bad sanitary condition of the nest, parasites, etc.; (5) amyl nitrite.

Reduced Feeding. — To reduce the feeding of the young doves one had only to limit the feeding of the parents, the latter refusing to regurgitate the food for the young when insufficiently fed. By this means one could not be certain of the amount eaten by the young unless the parents were not fed during a couple of days. In many of these cases the young died. In those cases where a partial starvation of the young was evident, one invariably found later, one or more fault-bars to correspond to it. In some cases the old birds were fed normally and one of their young was left with them as a control while the other bird was placed either in an incubator or under other nesting birds. The experimented bird could then be replaced with its parents and fed by them as little or as much as the experiment demanded. Twenty-four hours without food was invariably accompanied by the production of pronounced fault-bars (of type 1) in these birds. The control birds usually did not show these obvious defects (Pl. XIII., Figs. 6 and 7).

[1] Incomplete results of these experiments were communicated (1905) to Professor Duerden, who in his paper already cited (1906), wrongly credits the work to Drs. Strong and Whitman.

When adult ring doves were starved for periods of one to three days, *those portions of the feathers grown during those days showed well-marked fault-bars, one* (exceptionally two) *for each day of growth.* In such experiments the length of the feathers was measured at the beginning and again at the end of the starving period. For this experiment a control bird of similar age and condition was kept and fed normally in a cage alongside the starved bird. Measurements of the feathers of the control being taken also. The effect of three grades of feeding on the rectrix of a dove is shown in Pl. XIII., Fig. 6.

Many experiments have been made upon feathers which were replacing others that had been purposely removed. In these cases, the rectrices were pulled on the same day from two or more similar birds. After their new feathers had started to grow they were divided into experimental and control birds, and the low-feeding commenced. In Pl. XIII., Fig. 6, the effects of several days of starvation on such a feather have just been noted. This feather shows an absence not only of most of the *barbules* of the affected region but of the distal ends of the *barbs* as well. Careful inspection showed an occasional defective area in the control also.

The effects obtained by starving chicks — old or young — are in every way comparable to those just stated for doves, and a separate description therefore need not be given. Any considerable reduction of the food of doves and chicks will invariably produce well-marked fault-bars in many of their growing feathers.

The Feeding of Sudan III. — While the fat stain, Sudan III., was being fed to some young chicks for a quite different purpose, these were found to be producing defects similar to those produced by starving. This led to a careful study of what the stain could accomplish in the way of producing these abnormalities. *As a result of this study it can be said that when Sudan is fed in large amounts fault-bars are laid down in much the same manner as in the starving experiments.* The chief difference being that with Sudan the defects much more frequently take the form of constrictions (type 4) than of defective areas (type 1). Examples of the latter type are not uncommon, however, and were even large enough to appear in photographs (Pl. XIII., Fig. 13). That the

Sudan probably acts by reducing the actual nutrition of the bird is a conclusion that will be referred to again.

Birds for these experiments were kept under similar conditions in the three compartments of a specially constructed brooder. One lot of chicks served as control; another was fed a small amount of the stain; another a maximum amount. The number of fault-bars produced in any feather stand in this order (the number of feathers grown by the birds in the reverse order). The stain was fed in creamy milk (all the birds were given the milk). It was found that one had to feed the stain with the milk at the first time the milk was offered; otherwise the birds avoided it.

Effect of Mechanically Crumpling the Feather-germs. — In carrying through the experiments already described, a considerable amount of handling of the birds was unavoidable. It, therefore, seemed necessary to learn whether any of the defects, and particularly the few showed by the control, could have been produced by this procedure. This was tested by slightly marking in various ways one of the two birds of a brood; the marked bird (or in other cases the unmarked one) was then occasionally taken from the nest, its feathers measured, etc., as had been done in the earlier experiments. It was found that *this ordinary treatment was not followed by the production of evident defects.* When, however, the feathers were *strongly crumpled or broken in the region of growth, fault-bars resulted*, and by this means it was easy to *produce diffuse fault-bars at all levels of the feather* and this *quite independently of the usual time element involved.* That is to say, these large defects were laid down at irregular intervals, the space between two groups of defects depending upon the frequency with which the germs were crumpled. Crumpled primaries from the right wing are shown along with the corresponding ones from the left wing of a ring dove in Pl. XIII., Figs. 20–21.

General. — Several experiments of various kinds were next tried in order to learn whether the defects were in any way related to other conditions attending the birds in their nests. To this end, one of a pair of young birds were repeatedly taken from the nest and left exposed to cool air more than was the other; some birds were reared in foul nests, others in clean ones; some birds were infected with bird-lice, others not, and so on through the

range of factors which might conceivably be acting on the birds. *The results seem to fully justify the statement that none of these conditions can account for the defects*, neither in those of the experimented birds nor the occasional ones of the control. The net result of all the experiments thus far served apparently to demonstrate that the important factor in the production or non-production of the emphasized defects is *nutrition*. It did not, however, seem to be the only factor, for defects might sometimes be seen in feathers of well-fed birds. The difficulty thus presented was largely cleared up by the progress of studies in another direction (discussed under the next division of this paper). These studies had made it certain that normally *one defect is laid down in the germ for each day of growth*; while the examination of the various types of fault-bars had made it certain that the defective area of type 1 is a true representative of the defective line of type 3. The latter is, therefore, laid down daily as is the defective area. It follows that the proof of a causal relation between nutrition and *defective areas* is at the same time a proof that nutrition is causally related to the *defective lines* (that types 1 and 3 are merely different forms of the same defect I have already shown). And since the latter are present in all feathers from tip to tip, one for each day of growth, it is evident that the efficient cause (*i. e.*, nutrition) acts rhythmically. The few defective areas in control feathers could then be due, conceivably, to a slight emphasis of this normal internal rhythm. Since nutrition is a proved factor for the most extreme defects, it seemed extremely probable that it was also playing the chief part in the formation of all types of defects, including the extremely faint, elusive, and universal, defective lines. From this it would appear that the internal rhythm is a daily rhythm, and that it is able — like my experiments — to interfere with the nutrition of the feather-germ. This suggested *blood pressure* to me. To test this idea the experiments described in the following section were undertaken.

The Production of Fault-bars with Amyl Nitrite. — It is well known that amyl nitrite powerfully reduces the blood pressure in mammals. Some preliminary experiments on the effects of amyl nitrite on the circulation of the chick showed that when traces of it are inhaled, an immediate and extensive vaso-dilatation occurs.

Both the arterioles and veins of the comb, wattles, patagium, etc., are dilated. The strongest action, however, is exercised here as in mammals [1] upon the vessels of the viscera. This was ascertained by making considerable incisions through the body-wall so as to allow free observation; this was quickly followed by giving the drug. In other cases the bird was anæsthetized with ether before exposure of the viscera. The action of several drugs on the blood-pressure of birds has been studied by Dr. S. A. Matthews and the writer.[2] One of our tracings, showing the effects of amyl nitrite on the vascular pressure of a duck, is shown in text Fig. 5. A glance at this figure is sufficient to convince one that the

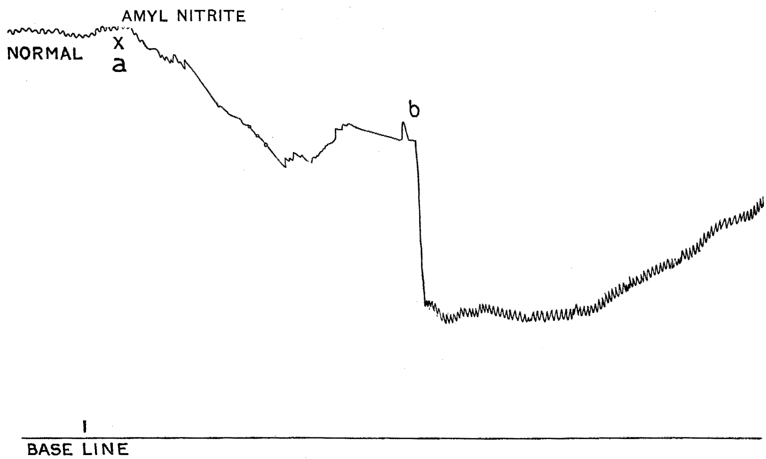

FIG. 4. Blood pressure tracing from the carotid artery of a duck. A normal pressure of 164 mm. Hg is here recorded. Amyl nitrite was given at *a* and again at *b*. The tracing shows a rapid fall in the arterial pressure to 50 mm. Hg.

alleged powers of amyl nitrite to diminish blood pressure is no myth.

To test directly the efficacy of amyl nitrite in the production of fault-bars the experiment was carried out in the following way: Two Plymouth Rock chicks of equal age (7 months) were taken at the time of their first moult; on the evening of the first experiment the distal ends of a number of their freshly expanding feathers were measured and *very carefully* cut away at a distance

[1] Cushny, C. A., "Pharmacology and Therapeutics," p. 470, Philadelphia, 1899.

[2] Riddle, O., and Matthews, S. A., "The Blood Pressures of Birds and Their Modification by Drugs," *Amer. Jour. of Physiol.*, Vol. XIX., June, 1907.

of 18 mm. from the skin. At 8:00 P. M. the birds were brought into the laboratory and were placed in similar large glass jars; a tube of amyl nitrite was broken in a bottle, the bottle was partially stoppered and placed in the jar with chick No. 1; the dose was regulated by means of the stopper; the comb and patagium serving as indicators. On the first night, however, in order to make sure that it was effective, the dose was increased until the bird toppled over unconscious; the bird was taken out and revived, replaced, and the supply of amyl nitrite slightly reduced. The bird now showed no discomfort, but chuckled and sang as if to express satisfaction; the birds were observed until 12 P. M. At 8:00 A. M. they were both released, returned to the green-house and fed as usual; at 8:00 P. M. of the same day they were again brought into the laboratory and the procedure of the previous evening repeated; at this time, however, No. 1 was not given sufficient of the drug to produce unconsciousness; on the following day at 8:00 A. M. they were again returned to the green-house; measurements of the rate of growth of some of their marked feathers were taken at intervals of two or three days during the next two weeks; feathers for sectioning were removed from birds I. and II. before the experiment began, and on the mornings following each experiment.

The result of this experiment leaves, I think, no room for doubt on one or two important points. When the parts of the feathers grown during the two days of the experiment had expanded, it was found that in No. 1, *two pronounced defects* (Pl. XIV., Figs. 22–23) *had been produced.* The feathers of No. II. were normal (Pl. XIV., Fig. 24). The sections tell the same story. The longitudinal section of a feather-germ (Pl. XV., Fig. 25) taken from the bird on the morning after the first experiment shows an abnormal region at about 2.5 mm. from the end of the feather. This undoubtedly represents the fault-bar produced on the preceding night.

There can be no question that amyl nitrite, when used as outlined above, is able to produce fault-bars in chicks. The question may of course be raised as to whether it does so by lowering the blood pressure or by some other means. In my opinion the probabilities that it does so are overwhelming, though its

capacity to form methæmaglobin in the blood and thus reduce the oxygenation of the tissues is a fact which should not be overlooked. But, if it be granted that a reduction by this means of the supply of oxygen to the tissues has a tendency to produce defects, then it becomes plain that *a reduction of the blood pressure alone must tend to produce them also*, since in any lowering of the blood pressure the amount of oxygen available to the tissues is decreased. It would seem moreover that we are justified in throwing out of consideration all other actions of amyl nitrite than those connected with the blood, since the inferior umbilicus of a feather-germ is a portal through which there enters from the body practically nothing except the blood-stream.

The Homologies of the Feather Defects or Fault-Bars.

The conclusive proof which has just been given that the fault-bars of feathers are produced by a reduced nutrition puts us in a position to state positively that these defects are the homologues of other defective growths of epidermal structures long known to be thus caused. Among these may be named: imperfections of the enamel of the teeth (dental hypoplasia); the grooving of the nails after illness; certain changes in the hair, particularly the weakening of the fibers of the wool of sheep which had been underfed; and the rings on the horns of many ungulates. It has already been suggested by Duerden that these structures are similar in nature to the feather defects. The proof of the suggestion lies, however, as stated above, in the determination of the cause of the fault-bars.

There should be added to this list such similar markings of epidermal structures as the concentric rings of annual growth found on the shields of many tortoises, and probably also the stratified hoof-formations of many animals.

It is worthy of note that the range of time involved between two of these successive abnormal productions varies from one day to one year. In the feather, however, the time varies only from one day to several days — different types of fault-bars resulting from the different periods. There is, nevertheless, but one cause for all these various formations, namely, a reduced food-supply, and this warrants our grouping them together.

Of greater interest than these known cases of epidermic response to nutrition are, in my opinion, similar responses which have as yet not been recognized in other tissues and organs. The constantly observable daily effects on feather structure of only slight "normal" daily reductions of nutritive conditions in the bird has fully convinced me that similar, and longer starving periods, and seasons of hibernation "normally" passed through by many animals, *cannot but produce definite and lasting marks in many of the tissues and organs of these animals.* (The effects may often, indeed, be so slight as to escape observation even with the microscope, but this does not negative their existence.) The writer believes that from this standpoint it would be very desirable to study the formation and growth of many tissues and organs; particularly such lamellar structures as ivory tusks, bone, certain ova, pacinian corpuscles, and doubless many others.

Feather Growth.

It was recognized at an early stage of these studies that accurate data on the *region* and *rate* of growth in the feather must be secured. Very few of the numerous writers on feather structure and development seem to have concerned themselves with either of these problems. The region of growth has of course been indicated in a general way (most definitely in "down") but its very restricted limit has not, heretofore, I believe, been sufficiently emphasized. The figures of Davies,[1] Haecker[1] and the still better ones of Strong[1] are, however, suggestive of it. Some observations and experiments on the rate of growth in chicks and doves are reported here.

The Region of Feather Growth. — A study of the growing tips of remiges and rectrices of ring doves, and of the primaries of the chick, shows that the region which produces the cells which enter into the formation of the barbules is less in extent than that which enters into the formation of the barbs (Pl. XII., Fig. 1); the barbule producing region representing less than 1.5 mm. of the entire length of these large germs. This region apparently does not begin at the extreme end (inferior umbilicus) of the feather, but slightly above it, and surrounds the wide portion of the

[1] *Loc. cit.*

pulp cavity (see figures). Others have pointed out that the *differentiation* of the barbs occurs later, *i. e.*, at a higher level than that of the barbules. There must be added to that the further fact that some of the cells which enter into the former *arise later* (at a higher level) than those which form the latter. A few observations on feathers from various birds, together with Strong's[1] figures of *Sterna*, afford considerable reason for believing that these statements on the region of growth in the chick and the dove may have among birds a very wide application.

The Rate of Feather Growth. — The rate of feather growth has not, so far as I am aware, been extensively or accurately studied. Cunningham[2] found that certain tail feathers of Japanese fowls grow at the rate of 3.5 mm. per day. Ostrich plumes are said to grow about one inch per week. In Plymouth Rocks my measurements show a very similar rate of growth. The rate varies greatly in different feather tracts of the bird; for example, in a Plymouth Rock it was, in the primaries, secondary coverts and body coverts, 4, 2.25, 1.75 mm. daily respectively. In general, the rate bears a rather definite relation to the ultimate length of the feather; and is less at the proximal than at the distal end of the feather. This is shown in the figures (Pl. XIII., Figs. 17–19); these indicate also the presence of fault-bars which are laid down at distances corresponding to the figures given above.

The ring dove shows a still more rapid feather growth. *Seven mm. of growth in 24 hours* has occasionally been recorded in the rectrices of these birds. The average for these birds is: rectrices 5–6 mm., primaries 5–6 mm., upper tail coverts 4 mm., primary coverts 4 mm. It will be recalled that *this is also the order of frequency for the appearance of the defective areas in the various feather-tracts.* This and kindred observations establish beyond doubt that the frequency of appearance of obvious fault-bars in feathers is directly related — one might almost say proportional to the rate of growth. Table I. gives some figures on the rate of growth in doves.

The Effect of Starvation on the Rate of Growth. — Starving conditions when brought to bear on growing feather-germs pro-

[1] "Development of Color," *loc. cit.*

[2] Cunningham, J. T., "Observations and Experiments on Japanese Long-tailed Fowls," *Proc. Zoöl. Soc. of London*, 1903.

TABLE I.

Bird.	10	11	12	13	14	15	16	17	= Age of Feathers in Days.
No. 83 starved	22	29	35	40	46	49	52	55	First 4 days = 6 mm. per day. Last 3 days = 3 mm. per day.
No. 97[1] control	24	31	38	43	49	54	58	63	First 4 days = $6\frac{1}{8}$ mm. per day. Last 3 days = $4\frac{2}{3}$ mm. per day.
	Length of feathers in mm.								
No. 20 starved	10	16	20	$24\frac{1}{2}$	28	32	34	36	First 4 days = $4\frac{1}{2}$ per day. Last 3 days = $2\frac{2}{3}$ per day.
No. 100 control	12	17	22	$27\frac{1}{2}$	$33\frac{1}{2}$	39	44	50	First 4 days = 5 per day. Last 3 days = $5\frac{1}{2}$ per day.

Showing rate of growth during seven days of starving and in control. The numbers in the first line at the top indicate the age of the feathers, *i. e.*, the number of days since the feathers of the previous plumage were removed. The first day of starvation is that between the tenth and twelfth days.

duce marked effects, some of which have been noted in connection with the production of fault-bars. It has been found that when the starving extends through periods of less than three or four days, that no diminution in the linear growth of the feather results (doves). The effects of such starvation are shown only, or at any rate principally, in that portion of the intermediate cell-layer which, as previously stated, produces the barbules.

If, however, the starving period is prolonged beyond the third day *a marked reduction of linear growth occurs* (Table I. gives exact figures for the growth of the rectrices of two starved, and two control birds). This means that *under poor nutritive conditions the formation of barbule-forming cells is first checked, and only under still more unfavorable food conditions will the growth of barb-forming cells be impaired.* This is a fact of the highest importance for an understanding of the origin of fault-bars, and also for a proper conception of the basis for the rhythms of pigmentation (formation of the fundamental bars). The proof of this is furnished by both microscopic and macroscopic study. We have already referred to Fig. 25 of Pl. XV., which shows the halted growth and division of barbule-forming cells in the region of the fault-bars.

In connection with these facts concerning the region and rate

[1] This bird was found to be in bad condition and died soon after this series of observations was concluded.

of growth we may consider one or two other related points. In the rectrices of doves the distance separating the point where the barbule cells arise, and a point at which they are practically completely cornified, is less than a centimeter. In his paper on the Development of Color, Strong's drawings show practically the same for *Sterna*, though he does not call attention to the fact. The measurements of the rate of growth (6 mm. per day) in the rectrices of the dove, when considered in relation to the distances separating the *origin* and *cornification* of a barbule cell, show that the *entire formation and differentiation of these cells occur in the short space of 24 to 36 hours.*

Since, moreover, 6 mm. of linear growth is accomplished in the 24 hours, 1 mm. would be grown in 4 hours. This would mean, then, that where a defective area (absent barbules) is 1 mm. in width that this area was produced in approximately 4 hours. This cannot be otherwise since the barbs — on which the barbules are borne — have been shown to grow steadily on during fault-bar producing conditions; certainly until the third or fourth day of starvation. *A defective area 1 mm. wide in the rectrices of doves indicates, quite certainly, very low nutritive conditions during a period of about four hours.*

The Nutrition of the Feather.

General on Feather Nutrition. — Hypotheses innumerable, concerning the nutrition of the feather, bridge the gap between the very queer conceptions of Dutrochet, Cuvier and Chadbourne. Dutrochet[1] asserted that the "blood-vessels are strangers to the phenomena of feather nutrition"; that a little liquid merely filters upward through the papilla. Cuvier[2] taught that the feather is laid down in a mould or matrix, the freshly added particle accomodatingly taking its place on the outside of parts already formed. Chadbourne[3] has informed us, however, that not only does the body establish blood and "vital" relations with the

[1] Dutrochet, R. J. H., "De la structure et la régénération des Plumes," *Journ. de Physique*, LXXXVIII., 1819.

[2] Cuvier, F., "Observations sur la structure et le development des Plumes," *Mem. de Muséum*, XIII., 1825.

[3] Chadbourne, A. P., "The Spring Plumage of the Bobolink with Remarks on 'Color Change' and 'Moulting,'" *The Auk*, Vol. XIV., No. 2, 1897.

feather-germ, but that the latter sustains and enjoys these same relations long after its maturity.

In discussing feather nutrition attention may be called to certain general nutritive relations which the feather bears to the surrounding parts. It has been pointed out by Poulton[1] that the feather follicle itself is merely a mechanism whereby "a better nutrition and support" of the feather is attained. The extreme vascularity of the papilla is another condition favoring a high nutrition. Further, the pulp cavity is widest and the epidermal parts thinnest at the region of most active growth (Pl. XII., Fig. 1).

Structural Relations Between the Feather-elements and the Blood. — A word is necessary here concerning the more intimate relations between the blood and the growing feather-elements. From Pl. XII., Figs. 4–5, much of these relations can be seen at a glance. It will be noted that (1) the capillaries are extremely numerous along the outer edge of the pulp; (2) of the epidermal structures the thin cylinder-cell layer lies nearest the capillaries; (3) the barb-forming region is narrowly separated from the capillaries by the cylinder-cell layer; (4) the barbule-forming region is still further removed from the capillaries; (5) lymph spaces extend presumably from the pulp to the outer sheath; (6) the large pigment cells occupy positions between the cylinder-cell layer and some barb-forming cells on the one hand and the barbule forming cells on the other.

It is obvious that the cylinder-cell layer occupies the favored position as regards all exchanges with the blood. It is an observed fact that its component cells continue to divide longer, *i. e.*, at a higher level in the feather, than any other part of the germ. Further, the barb-forming region is in a more favored position than the barbule-forming portion, the former being closer to the capillaries, and is also able to profit by adding to itself some of the newly formed cells of the cylinder-cell layer. That the barbules actually suffer more than the barbs under reduced feeding, etc., is proved by the structure of every fault-bar, and by reduced cell-division and growth of this region, as demonstrated by sections. This is also shown by the seven-day starving experiment already cited.

[1] Poulton, E. B., *The Quart. Jour. Micr. Sci.*, Vol. XXXVI., 1894.

From the above described relations it is plain that in case of a poor blood supply to the germ, the distant (more external) barbules would be first to suffer, since all their nutriment must filter through the cylinder-cell layer and around the barbs in order to reach them. The cylinder cells by their shape (usually spindle-shaped) are especially adapted to take up a maximum amount of food, so that parts peripheral to these will certainly suffer first.

It now becomes evident that the low blood pressure produced by amyl nitrite, and the low pressures (discussed below) occcurring normally, must exercise their chief effects on the distant barbule cells; a flow of lymph *from* the latter occurring as soon as the capillary tension is reduced. It is also plain that such a movement of the lymph must act upon these rapidly dividing cells in the same way as would an actual reduction of food with the blood pressure remaining constant. It is upon extremely actively dividing cells, which are removed by several cell diameters from the capillaries, that changes in the vascular pressure have an opportunity to exert an influence. Could more favorable conditions be imagined?

This daily rhythm of accelerated and depressed mitosis recalls similar cases in plants. It is well known that the cells of the root-tips of the Windsor bean (*Vicia faba*) show the greatest mitotic activity at noon — 11:00 to 1:00 daily. *Spirogyra* shows most rapid division at 1:00 A. M. and this period of maximum activity may here be delayed for several hours by cooling. In the plants it is difficult to determine the actual cause of the rhythm. In the feather cells, however, it is certain that the period of fewest mitoses is the period at which least food is available.

Blood Pressure Rhythms in Birds.

It must be said that a *daily blood pressure curve* for birds has not yet been produced. Probably no one, however, will doubt that there is a rhythm of high and low pressures in birds. Probably too, physiologists generally would expect the lowest point of the curve to correspond to the night — as in mammals. In fact, what we know of the factors upon which blood pressure depends in mammals, and what we know of the structures, habits and physiology of birds, would compel us to ascribe to the latter

a relative high pressure during the day and a low pressure at night. I give these *a priori* reasons for believing that a low blood pressure exists in birds at night because some may not be disposed to accept this as proved on my evidence alone.

To me it seems that the result of the amyl nitrite experiment proves much more than that a lowering of the blood pressure will produce fault-bars. *It is significant that the fault-bars produced by the amyl nitrite were superposed upon the defective lines* (and *not* on the fundamental bar between them) *belonging to the particular days of the experiment* (as was determined by subsequent examination). From this we can say with absolute certainty that *the fault-bars are normally laid down at night.* Furthermore, the smaller, "normal" low pressures must be accredited with the *same action* as these observed *extremely low* pressures and are, therefore, to be associated with the less obvious defective lines which are produced daily; they exert their action in the same direction, but to a smaller extent.

In this connection we may quote Tigerstedt's[1] statement concerning the blood pressures of poorly nourished animals. This author states that "schlecht ernährte Thiere haben einen niedrigern Blutdruck als kraftige Individuen derselben Art."

Finally, we may state the following inter-related facts, which go very far toward proving that a low blood pressure normally occurs at night in birds:[2] (1) Diminished feeding of birds produces emphasized fault-bars. (2) Artificially reduced (amyl nitrite) blood pressures produce equivalent defects. (3) The fault-bars are universal in feathers. (4) The fault-bars are produced at night. (5) The lowest daily temperature in birds occurs from 1:00 A. M. to 5:00 A. M. (6) Other physiological conditions of the bird seem to be favorable at night for the production of low blood pressures. (7) A lowering of the pressure would reduce the food-supply and have a tendency to produce defects.

Material for a direct demonstration of the daily blood pressure curve has unfortunately not been available. That its minimum

[1] Tigerstedt, R., "Lehrbuch der Physiologie des Kreislaufs," Leipsic, 1893.

[2] Simpson and Galbraith whose work is cited below find that the temperature curve of the owl (nocturnal) is reversed. If this is true the blood pressure curve of this bird may also be reversed, and the fault-bars (and light fundamental bars) produced probably in the afternoon.

occurs at night is shown, however, by the facts stated above. Duerden has been urged to obtain this curve from the ostrich. He writes me, however, that in his opinion the extremely nervous ostrich is not well adapted for such experiments.

Temperature Rhythms in Birds.

The daily temperature curve of birds was first obtained by Corin and van Beneden.[1] They found that the lowest temperature in pigeons occurs at 4:00 A. M. and the maximum at about 4:00 P. M. Their published curve is not altogether convincing because of the single species and few specimens examined, and because the temperatures at the close of their 24 hours' observation were always lower than at the beginning. This undoubtedly means that the first and highest part of the curve is too high. It was doubtless produced by the fright and struggles of the bird upon the first few insertions of the thermometer into the cloaca.

The only other observations on the temperature curve of birds which I have been able to find are by Simpson and Galbraith[2] who have recently obtained curves similar in most respects to those of Corin and van Beneden, and to those here reported by the writer. The work of these investigators showed, moreover, that in at least one nocturnal bird — the owl — there is a reversal of the diurnal temperature curve.

Corin and van Beneden reported that there is a fall in temperature from 8:00 A. M. till mid-day. Simpson and Galbraith did not find the same. This and other discrepancies in the results reported, together with the fact that only a few birds had been examined, led the writer to repeat the temperature observations on 16 birds. I, too, fail to find a fall in temperature between 8:00 A. M. and noon; only four showed a fall, nine a rise, and three no change in temperature between these hours. It is quite probable that by taking the temperature of the birds during every hour of the twenty-four, as it was done by Corin and van Bene-

[1] Corin, G., and van Beneden, A., "La Regulation de la température chez les pigeons," *Arch. de Biologie*, Vol. VII., pp. 265–276, 1887.

[2] Simpson, S., and Galbraith, G. G., "An Investigation into the Diurnal Variation of the Body Temperature of Nocturnal and Other Birds, and a Few Mammals," *Jour. of Physiol.*, Vol. XXXIII., December, 1905.

den, the normal condition of the birds was disturbed, and not being able to rest sufficiently at night they rested later — from 8:00 to 12:00 — and therefore showed a falling temperature during these hours.

The combined temperature curve for 16 birds, *i. e.*, 6 ducks, 5 ring doves and 5 chicks, is here reproduced (Fig. 5). The birds were under continuous observation for 48 hours. The curve expressses the temperature during the last 24 hours. The readings taken during the first 12 hours were found to be too high and unreliable; these were thrown out and the error of Corin and van Beneden avoided. This information was gathered with a view to obtaining additional data concerning the probable time of the lowest blood pressure in the bird. If the diurnal temperature

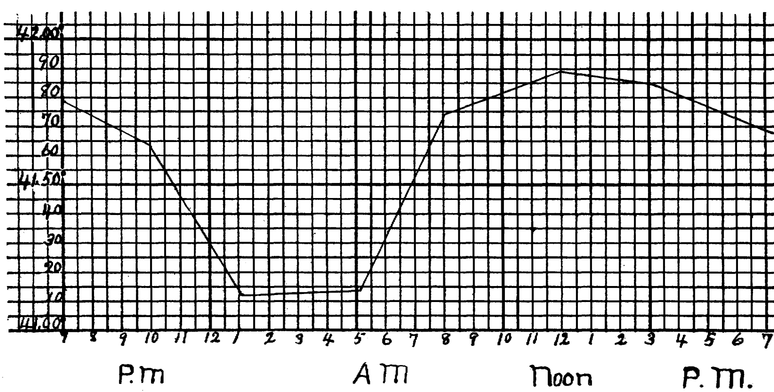

FIG. 5. Combined diurnal temperature curves of 16 birds.

and blood-pressure curves in birds are similar curves — as they are known to be in mammals — the temperature curve shown here indicates that the lowest blood pressure in birds occurs from 1:00 to 5:00 A. M. If the fall in the blood pressure is as sharp and of such short duration (3 to 6 hours) as is the very low temperature, it is easy to understand how it is that only a faint, narrow *line* is usually left to record its action.

Since the daily variation in temperature in birds is shown to be considerable — the above figures showing a lower temperature of about 0.7° C. for four hours of the day than for another twelve hours, — and since the fault-bars are produced during this low temperature, it may be asked whether the reduced temperature is caus-

sally related to the production of the fault-bars, and of the reduced pigmentation (light fundamental bars) soon to be considered. This is a possibility which should be considered in view of the fact that a reduction of temperature of 0.7° C. will, according to the rule of van't Hoff, reduce the speed of chemical reactions by one fifteenth. Furthermore, it has lately been stated by Tower[1] that in insects (where most experimental work on coloration has been done) "the most potent factors in the modification of color are temperature and moisture" (p. 214). I do not believe, however, that temperature is an important factor in the cases we are now considering. The various parts of the *growing region* of the feather undoubtedly have the same temperature and yet they grow unequally; this unequal growth of parts such as pigment, barbs and barbules under fault-bar producing conditions is really our whole problem, and has been proved to be caused by a factor — a reduced nutrition — which affects these parts to a different extent.

Relation of Pigment to Fault-Bars and Nutrition.

The position of the pigment cells between the cylinder-cell layer and the barbule-forming cells has already been pointed out. It will be noted, too, that their processes reach the barbule cells and are, in fact, rather closely applied to them at the time the latter secure their pigment. In just the same way that a lack of nutrition checks the production of barbule-forming cells, it reduces the amount of pigment formed and taken up by the barbule cells.

It seems very certain that this last statement is true, for a macroscopic examination of the completed feather shows a deficiency of color in this region; and some parts of the cross-sections of such areas of adult feathers show plainly upon microscopic examination that less pigment was produced there. It is, however, very difficult to show by microscopic means that in the living, growing feather-germs less pigment is being produced, because of the fact that the pigment cell processes are never able to even approximately empty themselves, and always appear

[1] Tower, W. L., "Evolution in Chrysomelid Beetles of the Genus *Leptinotarsa*," Carnegie Institution, 1906.

black. Quantitative estimates by this method are therefore not easy. Pls. XII., Fig. 4, and XV., Fig. 26, and text Fig. 2 show, very clearly that in these two types of fault-bar there was practically a suspension of pigment production during the fault-bar producing period.

In Pl. XIII., Fig. 14, is shown a feather from a Japanese turtle dove. Here a continued reduction of the pigmentation of nearly all of the primaries followed a period of malnutrition. This period is indicated in the primaries by a narrowing of the feather-vane at one point and by a few fault-bars. The rectrices of the same bird, recorded this starving period by means of a few very obvious defects. (The actual starving of this bird was neither intended nor observed, but this interpretation seems unquestionable). In other cases it has been observed that a very strong fault-bar sharply separates a pigmented part of a feather from an unpigmented part. Pl. XIII., Fig. 10, shows such feathers from a pigeon. The part of the feather proximal to the defects is unpigmented, although it normally bears pigment.

The observation that fault-bar producing conditions may occasionally weaken or apparently permanently destroy the pigment-producing power of the feather would seem to be of much importance; but the mechanism of this action is wholly unknown. The fact that these fault-bars are areas provided with a reduced amount of pigment, and the further fact that nutrition stands in a causal relation with the fault-bars — and the reduced production of pigment — suggests however some interesting relations of the melanin pigment and the food. Indeed one cannot review the results of these studies without finding some evidence that *melanin arises not from hæmaglobin but from the proteids of the foods (serum) or of the cell.* Recent work in physiological chemistry has furnished much evidence in favor of this view. It would seem that in the birds the production of feather pigment stands in a rather immediate relation to the foods, and even to fluctuations in the food supply.

In regard to the behavior of *lipochrome* pigments, it may be said that, though a thorough study has not been made, they seem to take up their positions without regard to the fault-bars and fundamental bars. Where the word "pigment" is unqualified in this paper, *melanin* is meant.

The Meaning and Cause of Fault-Bars and Fundamental Bars.

The facts bearing on fault-bars and, indeed, on fundamental bars, have already been stated. It remains only to point out their inter-relation and significance.

It has been shown that there exists in certain elements of the rapidly growing feather-germ a rhythm of growth which is dependent upon the nutrition. Those parts of the feather which are grown under the poorest nutritive conditions show defects — *fault-bars* of all grades of imperfection. Those regions of the feather — normally the larger part — which are produced while growth and cell-division are in full swing, form the *fundamental bars.*

In pigmented feathers the development of pigment is modified at night along with the other elements and there results a structurally weakened and less pigmented area. This region we have thus far spoken of as a fault-bar; since, however, this same area has been found in some cases to lose considerable pigment without having lost any barbules, we speak of it also as a *light fundamental bar.* On the other hand, pigment develops uninterruptedly during those hours of the day when growth is most rapid, and the well-pigmented portion of the feather then laid down forms the *dark fundamental bar.*[1]

Fault-bars and fundamental bars are universal in feathers (in white feathers there is, of course, no rhythm of pigmentation), and are direct expressions of the rhythmic nutritive[2] conditions. The poorest food conditions obtain at night. A reduced blood pressure, probably much emphasized in the later hours of the night is to be regarded as a factor (by affecting the nutrition) in

[1] This is a complete confirmation of a view arrived at by Professor Whitman in 1903 (not published until 1907). From observations quite different from these, he had reason to believe that the bars might be "zones of daily growth (light = day; dark = night, or vice versa)."

[2] The words "food" and "nutrition" are used in a general sense and include *oxygen.* It is not improbable that the slower growth and cell division and the diminution of the production of melanin pigment under fault-bar producing conditions are, in part at least, due to a reduced oxygen supply. In all my experiments, and in every lowering of the blood pressure, the oxygen supply of the tissues is diminished. The probability here stated grows in importance when it is remembered that free oxygen plays an important rôle in the germination of seeds, the segmentation of ova (mitotic activities), and probably also in the oxidation (Samuely) of tyrosin (Gessard, v. Fürth and Schneider) to form melanin.

the production of all fault-bars and of the light fundamental bars; while the better normal nutrition of the day and of the first part of the night is associated with the production of the dark fundamental bars.

The large light and dark transverse bars with which we have all long been familiar in Plymouth Rock fowls, in hawks, in jays, etc., are of course not the light and dark fundamental bars with which this work deals, and are not each the growth of a day or night; it is perfectly evident that in them a single broad black or white bar may include the growth of two, three or more days. But even these broad bands of white and black may later be found to bear secondary or derivable relations to the fundamental bars.

The alternating light and dark fundamental bars are only rarely seen in their fullest development, *i. e.*, as well defined alternating bands of lighter and darker color. Experience would indicate that they are found to best advantage in pale feathers rather than in those with a superabundance of pigment. The separation of the feather into the faint defective lines, and the broader well-grown areas is, however, easily found in all feathers. The light and dark fundamental bars are shown in Pl. XIII., Figs. 15–16.

Discussion.

It is then through such a mechanism as has been described in the foregoing pages that the melanin pigment of feathers comes to be laid down in alternating light and dark transverse bars.

In concluding the presentation of this subject, I shall attempt no extended discussion of the relation of this to similar work, nor of its relation to general biological problems. A few statements of this import, touching upon that part of this work which deals with color-formation may, however, not be too wide of the mark.

It can be said that thus far those who have essayed to carry the puzzling facts and phenomena of animal coloration from the dark fields of *heredity* into the proved and clarified domains of *physiology* have met with only partial success at best. The efforts of Graf and of Loeb in this direction were mentioned in my introductory statement as among the most successful.

Graf's contribution is that in leeches certain tissues are found to offer greater resistance than others to the migrating "excre-

tophores" which contain a pigment. At the points of resistance chiefly the muscles of the body wall — the pigment is piled up and contributes strikingly to the color pattern.

The earlier work of Eisig[1] on the coloration of the Capitellidæ presents certain analogies to the work just mentioned. This investigator states that in these forms certain color areas arise through the transformation of blood-disc clusters which lie between the cuticle and hypodermis; the transformation being due to stagnation of the blood flow after invasion by excretory (pigment) particles. Each of the two works just cited undoubtedly throws much light on the coloration of the forms studied; but it may also be remarked that the *origin* of the pigment in both cases is still somewhat in question, and that the results do not seem to be of wide application. In fact, it is now evident that no theory which considers pigments as waste products, tossed about by the circulation until they find some sort of excretion, can be of general application.

Certain pigmentary colors in the color-patterns of several orders of insects have been pointed out from time to time by various workers as being correlated with certain structures — spiracular openings, venation, attachments of muscles in the body wall, positions of other internal organs, etc. In all these cases, however, little more than "correlation" has been accomplished. We have yet, I believe, to obtain anything approaching a complete and unequivocal explanation of any of these associations.

The facts observed by Loeb on the chromatophores in the yolk-sac and embryos of *Fundulus* are perhaps the most helpful of the few similar studies thus far made on vertebrates. The observation of an actual and definite *migration of entire chromatophores* (of two types) into a definite color pattern, and this under some (?) influence exerted by the *circulating blood* forms two important steps toward a physiological explanation of the coloration in question. It should not be overlooked, however, that the final step would involve a much better knowledge of the nature of the influence which the blood brings to bear on the chromatophores; and further it may be said that in the explanation of the color-patterns of animals it seems at present that this mechanism, too, has a rather restricted application.

[1] Eisig, H., "Die Capitelliden," Naples, Monograph, 1887.

Zenneck[1] has shown that in the case of the ringed-snake (*Trophidonotus natrix*) the three longitudinal rows of spots in the adult correspond to the positions of three subcutaneous blood-vessels of the embryo. This work in some respects parallels that of Loeb, but with the important difference that Zenneck finds the pigment aggregating about degenerating vessels only, while Loeb found that the circulation of the blood in the living vessel was essential to the process. That this interesting observation, too, merely throws light on a detail — not a fundamental — of animal coloration, seems quite certain.

A paper by List[2] describes as universal for vertebrates the relations between pigment and blood-vessels which were later described by Loeb for *Fundulus*. His rather theoretical work is based on the erroneous view that the pigments of vertebrate color-patterns are carried into the integument by the leucocytes of the blood. That his conclusions are wrong — particularly as applied to birds — is proved by the results set forth in this paper, and by much other evidence as well.

Following this very brief statement and criticism of previous work, we may perhaps be pardoned a concluding word concerning the scope and limitations of the present contribution. The limitations of the work here presented are, indeed, as obvious as they are real, but to hold them in bolder relief for a moment may prove of some slight service to those — if such there be — whose eyes are ill-accustomed to the lights and shadows which play upon this particular section of the borderland of heredity and physiology.

1. The origin and distribution of melanin pigment only has been considered. This includes nearly all the black, brown, and reddish-brown pigments of animals. It is clearly the prevailing integumentary pigment of mammals, birds and many other groups.

2. The birds only have been used as a basis of study.

3. Very few of the actual groupings of melanin pigment in the birds receive an *immediate* explanation through the processes described. It seems very probable, however, that many com-

[1] Zenneck, J., "Die Anlage der Zeichnung und deren physiologische Ursache bei Ringelnatter-embryonen," *Zeitschr. wiss. Zoöl.*, LVIII., 1894.

[2] List, H. J., "Ueber die Herkunft des Pigmentes in der Oberhaut," *Biolog. Centralbl.*, X., 1891.

plex patterns will be found to have been built directly out of the fundamental bars.

On the other hand, the following definite things have been accomplished in the reduction of the "inherited" color-phenomena of birds, to an intelligible, physiological basis.

1. All the feathers of all birds possess — usually in addition to other coloration — regular segmental color-characters which represent (roughly speaking) days and nights of growth.

2. The darker portions are produced by day and the first part of the night, the lighter portions chiefly at night between 1:00 and 5:00 A. M.

3. A low blood pressure at this latter period produces a reduced nutrition.

4. This reduced nutrition causes a slower rate of growth of most — but not all — of the feather elements. The pigment is one of the elements which suffers a reduction.

5. The pigment (and certain other parts) is reduced in its rate of production relative to growth in certain other parts, because of the less favorable relations which the pigment producing cells bear to the nutriment carried by the blood.

The writer believes that these findings give a clearer and more penetrating view of the genesis of a color character than has heretofore been obtained. In no previous case has the attempted analysis included *reasons for quantitative variations in pigment production.* In fact, the whole matter of the origin of pigment — as distinct from the problems of its distribution or placement — has in all these cases been either left untouched, or only waste products acting as pigments have been considered; or again, gratuitous assumptions have been made of its origin from hæmoglobin.

Probably, however, the chief value of what is here presented lies not in the moiety it has taken from the province of heredity and added to that of physiology, but in the *absolute starting point which it supplies for evolutionary studies of the color-characters of birds.* Whitman[1] has already pointed out that the *fundamental bars, whose significance is here made known, are to be re-*

[1] Whitman, C. O., "The Origin of Species," *Bull. of Wis. Nat. Hist. Soc.*, January, 1907.

garded as the primitive avian color-markings. He further states that "from these fundamental feather-bars or their secondary derivatives a multitude of specific characters have been evolved by gradual modification."

Summary.

1. Fault-bars, or feather defects presenting five rather distinct types, have been found and described.

2. The fault-bars occur "normally" in all bird groups, in all plumages, in all feather tracts, and in all individual feathers.

3. Fault-bars can be readily produced experimentally by reduced feeding; by the feeding of the fat stain Sudan III., which seems to "tie up" certain foods; by very strong mechanical crumpling sufficient to break the tissues and blood vessels; and by lowering the blood pressure with amyl nitrite.

4. Fault-bars are produced only by such agencies as bring about poorer nutritive conditions in the feather-germs.

5. Homologues of the fault-bars are to be found in the several epidermal growths of animals which reflect better and worse nutritive conditions. Other tissues than the epidermal may be found to show structural effects of rhythms of growth.

6. The region of growth in the feather is very restricted, being narrower for the barbule — less than 1.5 mm. in very large feather-germs — than for the barb-producing region.

7. The rate of growth in the feather, as compared with growth elsewhere in the organism is extremely rapid, and varies within wide limits. Up to a certain point the rate bears a rather definite ratio to the ultimate length of the feather, being fastest in those feathers which become longest.

8. Under "starving" conditions, the rate of linear feather-growth is not affected until the third or fourth day; after this the rate falls rapidly (doves).

9. The structural relations between the various feather elements and the blood are such that not all the parts are equally favorably situated to obtain nutriment from the blood; the shaft, barbs, pigment, barbules, inner and outer sheaths occupying advantageous positions in the order named.

10. Previous results showing that the lowest (daily) temperature of birds occurs in the early hours of the morning (1:00 to 5:00 A. M.) have been confirmed.

11. A daily blood pressure rhythm with a minimum pressure occurring doubtless between 1:00 A. M. and 5:00 A. M. is present in birds.

12. The reduced nutrition brought about daily by this minimum blood pressure; the disadvantageous position, in relation to the blood, of the pigment and barbule elements of the feather; together with the very rapid rate at which feathers grow, furnish the complex of conditions which bring unfailingly into existence a fault-bar, and to a more or less appreciable extent a light fundamental bar, at perfectly regular intervals in the entire length of every feather formation.

13. The melanin pigment of the feathers of birds shows, under favorable conditions, quantitative variations of the pigment produced in response to changes in the available food supply. This is an additional evidence that this pigment is not a derivative of hæmoglobin, but of the serum or cell proteids.

14. The light and dark fundamental bars are universal in feathers (Whitman) and have been shown by the writer to represent different conditions and periods of growth; the dark fundamental bars (of pigmented feathers) being expressions of growth and pigment production under the most favorable conditions; these conditions obtain during the day and the first part of the night; on the other hand, the light fundamental bar is brought into existence, as stated above, by fault-bar producing conditions, *i. e.*, by the low nutritive conditions which obtain during the later hours of the night.

15. These results furnish a description in the terms of physiology, of the mechanism of the "inheritance" of certain fundamental color-characters of all birds.

16. The fundamental bars furnish the starting point for all evolutionary studies on the color-characters of birds.

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ABBREVIATIONS.

b. fault-bar.
bb. barb.
ble. barbule.
c. region of reduced pigmentation.
cap. capillaries.
if. inferior umbilicus.
i sh. inner sheath.
lb. longitudinal fault-bar.
m.b. basal membrane.
m. modified region.
n. nucleus.
p. pigment cell.
pc. process of pigment cell.
pl. pulp.
rh. rhachis or shaft.
tu. outer sheath or tunica.

EXPLANATION OF PLATE XII.

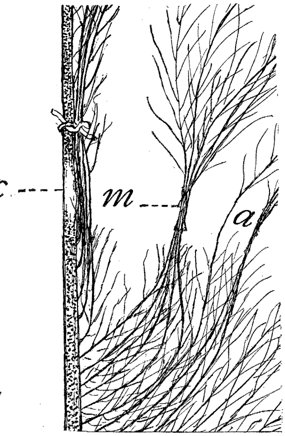
FIG. 1. Diagrammatic representation of rectrix of dove in longitudinal section. Barbule cells are formed between *x* and *y*; barb cells in the region of *z*; cornification complete at *w*; Fig. 5, Pl. XII., from region *v*. × 14.

FIG. 2. Semi-diagrammatic cross-section of a feather-germ. × 50.

FIG. 3. Longitudinal section of feather-germ of *Cardinalis*; constrictions *a* invading pulp. Drawn with aid of camera lucida. × 20.

FIG. 4. Modified region of a feather from a "starved chick." Effects of lack of food are seen in the loss of barbules in the fault-bar region *a*; in a very peculiar massing and cornification of barbs at *m*; and in an almost total absence of pigment in the shaft at *c*. × 8.

FIG. 5. Camera lucida drawing of a segment of the cross-section of the rectrix of a dove, taken at the level *v* in Fig. 1. No attempt was made to indicate the cellular structures of the pulp; the red blood corpuscles within the capillaries also omitted. Only such capillaries were indicated as contained red blood cells and thus made their nature certain. Undoubtedly still others were present. The line across the four ridges indicates the plane of section of Fig. 25, Pl. XV. × 360.



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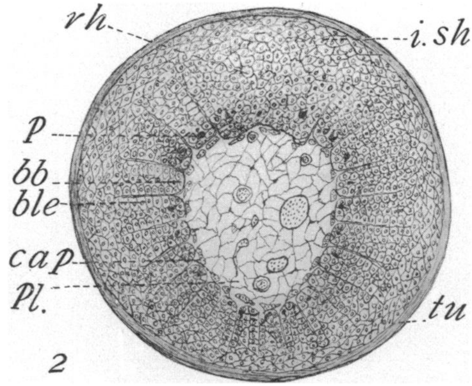

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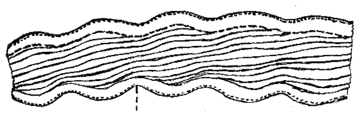

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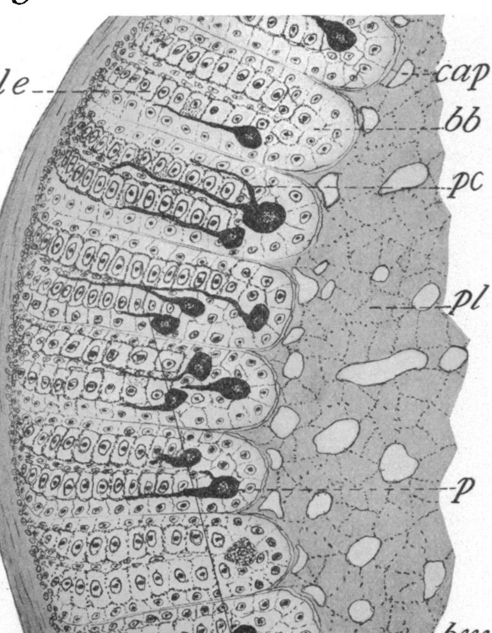

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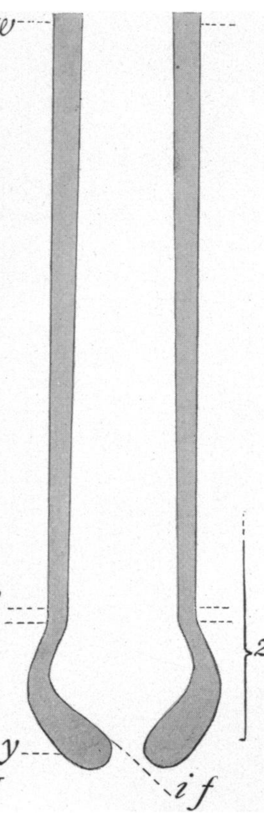

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Explanation of Plate XIII.

All figures are direct prints on solio paper, therefore white shows as black, and *vice versa.*

Fig. 6. From a young dove which fed normally during the first week after hatching, poorly fed during the second week, and fed still less during the following ten days.

Fig. 7. Tail covert of an underfed dove. "Abrasions" *a* occurring at the fault-bars. Those at *d* produced artificially by pulling on distal end of barbs.

Fig. 8. Body covert (from nape of a Sudan-fed chick) with wavy band crossing it; before this region expanded it existed as a constriction (fault-bar type 4) of the feather-germ.

Fig. 9. Series of the same modifications in body covert of *Cardinalis.*

Fig. 10. From region of crop of pigeon. A fault-bar occurs at *b* which sharply bounds a peripheral pigmented and a proximal unpigmented portion.

Figs. 11–12. From tail of English sparrow. No. 11 has an incompletely differentiated, unexpanded portion *b* at a point where the feather which grew beside it (Fig. 12) shows a typical fault-bar.

Fig. 13. Primary of chick (juvenal plumage) showing fault-bars produced by feeding Sudan III.

Fig. 14. Primary of Japanese turtle dove. A fault-bar at *b* separates a more pigmented distal from a less pigmented proximal part. The entire feather is narrowed from *b* to *a* showing that poor nutritive conditions prevailed throughout this period. This region seems, by the method of photography here employed, to be more heavily pigmented than other parts; this is due not to actual pigmentation but to an opacity caused by the extreme cornification and lack of separation of the feather-elements.

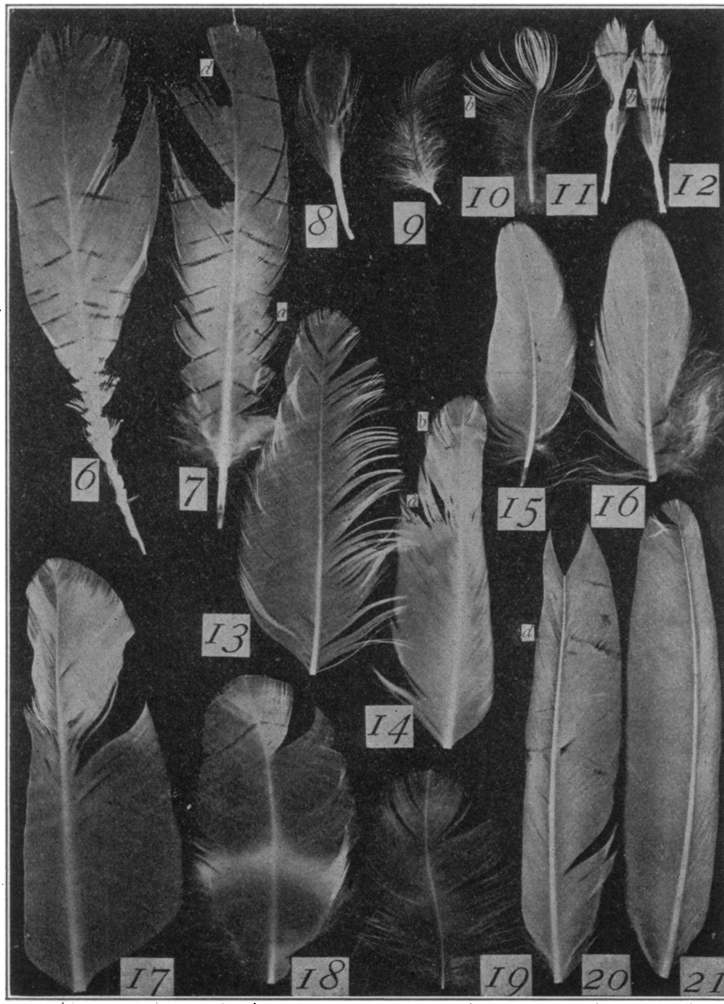
Fig. 15. Showing light and dark fundamental bars in body covert of a Japanese turtle dove.

Fig. 16. Fundamental bars in wing covert of pigeon (these rather faint bars and those of Fig. 15 are here practically lost. The method of direct printing here employed is not equally good for the fault-bars and fundamental bars).

Figs. 17–19. No. 17 — primary, No. 18 — secondary covert, and No. 19 a body covert from crop region of a chick. The difference in distance between successive fault-bars is an index of the rate of growth and bears a definite relation to the ultimate length of the feather (the fault-bars in Fig. 19 are practically lost in the reproduction), though they were very plain in the specimen.

Fig. 20. Crumpled primary of right wing of dove showing fault-bars at *d.*

Fig. 21. Control of above; the corresponding primary of the left wing of the same dove.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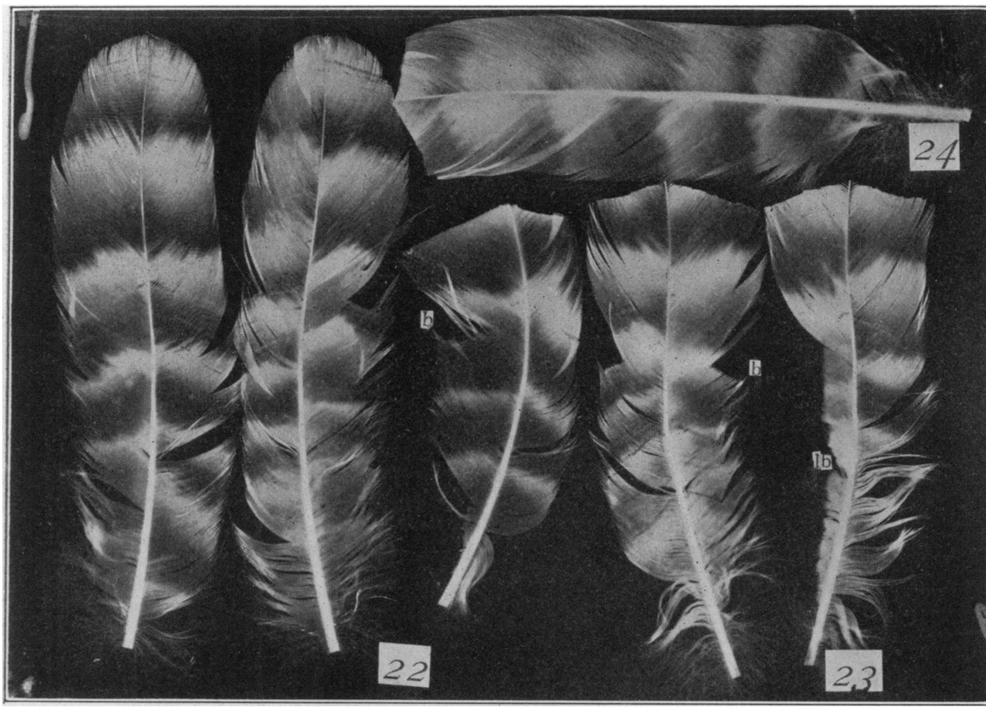
EXPLANATION OF PLATE XIV.

FIG. 22. Four rectrices of chick "dosed" with amyl nitrite on two succeeding nights. (Several feathers had their tips cut off at approximately 18 mm. from the skin, so as to be able later to identify the region affected by the low blood pressure produced.) Points marked *b* are the fault-bars produced on the nights of the experiment.

FIG. 23. A fifth rectrix which in addition to the usual fault-bars shows a longitudinal fault-bar for *lb* beginning with the second night of the experiment.

FIG. 24. A rectrix from the control chick. These feathers show no defects.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b
b
b
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23

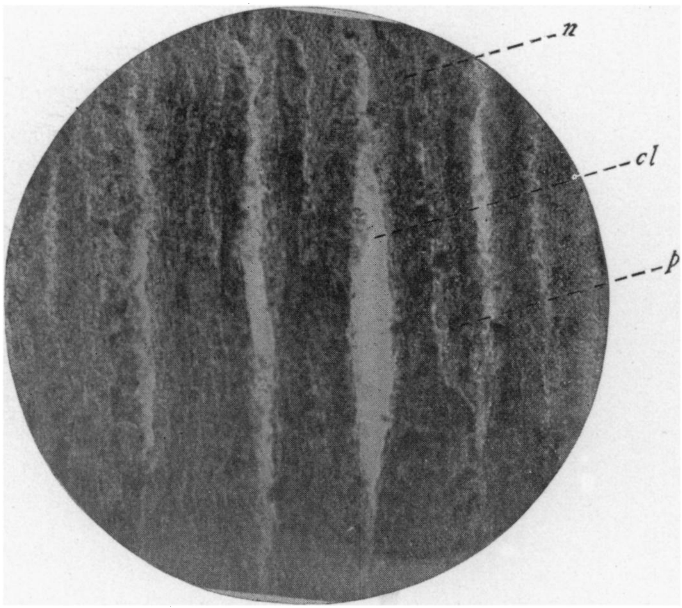
Explanation of Plate XV.

Photomicrographs.

Fig. 25. Longtudinal section of a fault-bar region soon after fault-bar producing conditions were past. This being a tail feather, from the chick which was given amyl nitrite, taken four hours after the chick was removed from the amyl nitrite atmosphere.

This "bar" occurs about 1.5 mm. from the extreme proximal tip of the feather and occupies a position which may be better understood by reference to Fig. 5, Pl. XII. It is a region on the border line of barb, barbule and pigment producing cells. Cell outlines in such a region are usually indistinct; the nuclei *n*, however, have not photographed perfectly, so that an idea of the looser, more irregular arrangement of the cells is only imperfectly given. That an actual reduction of growth occurred here, is, however, beautifully shown by the large clefts *cl* or clear areas of the pulp which have here been left between the several barb-formations (ridges). Killed in Kleinenberg's picro-sulphuric mixture, and stained in hæmatoxylin and eosin. $\times$ 300.

Fig. 26. Fault-bar *b* with reduced pigmentation of all elements of the feather, including the shaft *c*, in a rectrix of the ring dove. $\times$ 40.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b
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